

BALD EAGLES AND SEA OTTERS IN THE ALEUTIAN ARCHIPELAGO: INDIRECT EFFECTS OF TROPHIC CASCADES

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Abstract. Because sea otters (*Enhydra lutris*) exert a wide array of direct and indirect effects on coastal marine ecosystems throughout their geographic range, we investigated the potential influence of sea otters on the ecology of Bald Eagles (*Haliaeetus leucocephalus*) in the Aleutian Islands, Alaska, USA. We studied the diets, productivity, and density of breeding Bald Eagles on four islands during 1993–1994 and 2000–2002, when sea otters were abundant and scarce, respectively. Bald Eagles depend on nearshore marine communities for most of their prey in this ecosystem, so we predicted that the recent decline in otter populations would have an indirect negative effect on diets and demography of Bald Eagles. Contrary to our predictions, we found no effects on density of breeding pairs on four islands from 1993–1994 to 2000–2002. In contrast, diets and diet diversity of Bald Eagles changed considerably between the two time periods, likely reflecting a change in prey availability resulting from the increase and subsequent decline in sea otter populations. The frequency of sea otter pups, rock greenling (*Hexagrammus lagocephalus*), and smooth lumpfish (*Aptocyclus ventriosus*) in the eagle's diet declined with corresponding increases in Rock Ptarmigan (*Lagopus mutus*), Glaucous-winged Gulls (*Larus glaucescens*), Atka mackerel (*Pleurogrammus monopterygius*), and various species of seabirds during the period of the recent otter population decline. Breeding success and productivity of Bald Eagles also increased during this time period, which may be due to the higher nutritional quality of avian prey consumed in later years. Our results provide further evidence of the wide-ranging indirect effects of sea otter predation on nearshore marine communities and another apex predator, the Bald Eagle. Although the indirect effects of sea otters are widely known, this example is unique because the food-web pathway transcended five species and several trophic levels in linking one apex predator to another.

Key words: Aleutian Islands, Alaska, USA; Bald Eagles; coastal marine communities; diets; *Enhydra lutris*; *Haliaeetus leucocephalus*; productivity; sea otters; trophic cascades.

INTRODUCTION

Attempts to understand food-web dynamics have led to two sets of contrasting perspectives, one being the relative importance of bottom-up vs. top-down forces (Hunter and Price 1992) and the other being the importance of direct vs. indirect interactions (Polis et al. 2004). Although bottom-up processes have long been the focus of most studies of food-web dynamics, consumer-mediated effects on the demography and behavior of prey also are well known. In contrast, the indirect consequences of these species interactions are less well known. Furthermore, most research on the indirect effects of apex predators has focused on “trophic cascades,” the progression of consumer-mediated influences downward through lower trophic levels

(Paine 1980, Carpenter and Kitchell 1993). Trophic cascades may cause changes in abundance, distribution, and productivity of autotrophs, the effects being positive or negative depending on whether the number of trophic levels in the interaction chain is odd or even (Fretwell 1987). While there is evidence for trophic cascades from diverse ecosystems (Pace et al. 1999) and more recent studies have assessed the strength of trophic cascades on species and ecosystems (Shurin et al. 2002, Borer et al. 2005), the indirect influences of trophic cascades on different species is largely unstudied.

The sea otter (*Enhydra lutris*)–kelp forest system has provided important insights into the effects of this mammalian predator on food-web and ecosystem dynamics. The system's utility is due in part to a series of historical events: the near extinction of sea otters during the maritime fur trade (Kenyon 1969); their spatially asynchronous recovery from a few widely scattered surviving colonies following protection (Kenyon 1969, Riedman and Estes 1990); and the recent large-

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scale collapse of sea otter populations in southwest Alaska (Doroff et al. 2003, Estes et al. 2005). Sea otter populations existed at or near carrying capacity throughout most of southwest Alaska until about 1990, at which time they began to decline precipitously. By the late 1990s sea otter numbers had declined by roughly an order of magnitude across the entire Aleutian Islands (Doroff et al. 2003), and the nearshore ecosystem shifted from a kelp-dominated to a deforested state (Estes et al. 2004). These events have made it possible to contrast systems with and without sea otters in the Aleutian Islands where the boundaries of islands are discrete, and the ability for sea otters to move among islands is limited because of great distances and water depths.

Comparisons between islands with and without sea otters have revealed that otters maintain the kelp-forest ecosystem by way of a trophic cascade (Estes and Palmisano 1974). This occurs because sea otters eat sea urchins (*Strongylocentrotus polyacanthus*), sea urchins eat kelp, and sea urchin populations that are unregulated by otter predation can become sufficiently abundant to overgraze kelp forests. The presence of kelp-dominated vs. deforested communities in the Aleutian Archipelago is highly predictable based on the presence or absence of sea otters (Estes and Duggins 1995). These alternate community states (Steneck et al. 2003) potentially influence other species through at least three ecosystem-level processes: changes in primary production, the presence or absence of a three-dimensional habitat (i.e., the kelp forest), and altered water flow due to buffering effects of the kelp forest on waves and currents (Estes 2005). For example, the growth rates of filter-feeding mussels and barnacles are enhanced 2–3 fold in otter-dominated communities because of increased production and elevated concentrations of particulate organic matter in the water column (Duggins et al. 1989). In addition, fish densities in kelp forests are elevated substantially in otter-dominated systems (Reisewitz et al. 2006), and the diet and foraging behavior of Glaucous-winged Gulls (*Larus glaucescens*) differ greatly between areas with and without sea otters (Irons et al. 1986).

Bald Eagles (*Haliaeetus leucocephalus*) are a *K*-selected species with a low reproductive potential and high survival rates after the first year of life (Buehler 2000). They occupy breeding territories as far north as central Alaska and Yukon Territory and as far south as Arizona and Florida in the United States and Baja California, Mexico (Stalmaster 1987). The western extent of their geographic range occurs in the western Aleutian Islands, Alaska, USA (Gibson and Byrd 2007). They are top-level predators that breed in marine, estuarine, and freshwater ecosystems and acquire most of their prey from aquatic environments (Stalmaster 1987). They have relatively small breeding territories and tend to remain on these territories year-round, provided the surrounding water bodies do not freeze

during winter (Garrett et al. 1993). Because their breeding territories are small, they have evolved as opportunistic feeders (Watson et al. 1991), and their diets reflect the abundance of prey that are available to them (Buehler 2000). As a result, their diets tend to be diverse, and they show a remarkable level of dietary plasticity from one region to another. In the Aleutian Islands they acquire >90% of their prey from nearshore marine communities and feed on a diversity of birds, mammals, and fish (Sherrod et al. 1976, Anthony et al. 1999).

The Bald Eagle's close link to nearshore marine communities in the Aleutian Islands (Anthony et al. 1999) puts them in close association with sea otters and the otter's influence on these communities. For example, sea otter pups may comprise as much as 15% of the Bald Eagle's diet during the nesting season (Sherrod et al. 1975, Anthony et al. 1999). In addition, Bald Eagles prey upon kelp forest fishes, particularly rock greenling (*Hexagrammus lagocephalus*), and several species of marine birds (Anthony et al. 1999). Consequently, the purpose of this study was to investigate the potential influence of the recent decline of sea otters on density, productivity, and diets of Bald Eagles in the Aleutian Archipelago. We predicted that the otter decline would cause a decline in eagle prey, and eagle diets would change accordingly. We also predicted that the decline in prey abundance would have negative effects on productivity and density of breeding pairs.

METHODS

Study area and study design

The Aleutian Archipelago comprises over 200 named islands extending 1800 km westward from the tip of the Alaska Peninsula toward Asia, and separates the North Pacific Ocean from the Bering Sea. Maritime tundra characterizes the vegetative communities on all islands. Ocean-derived nutrients drive organic production, which is reflected by an abundance of marine fauna and a relatively impoverished terrestrial biota (Croll et al. 2005). Our study was conducted on four islands, two each in the Andreanof (Kiska and Tanaga Islands) and Rat Island (Kiska and Amchitka Islands) groups.

Sea otter populations were rare or absent throughout most of the Aleutian Archipelago through the 1930s but increased to levels near equilibrium density from the 1960s through the late 1980s. Sea otter populations were at or near carrying capacity throughout the Andreanof, Delarof, and Rat island groups of the Aleutian Archipelago through the late 1980s (Kenyon 1969, Riedman and Estes 1990). Sea otter numbers began to decline throughout this region ca. 1990, and by the late 1990s, they had decreased by about 10-fold (Estes et al. 1998, Doroff et al. 2003). The decline in sea otters in the western Aleutians was exemplified by the precipitous decline in otter populations on Adak Island, one of our study sites (Fig. 1), and this pattern of decline was similar among all islands. The ensuing change in the

kelp-forest ecosystem from being kelp dominated to extensively deforested occurred abruptly across the Aleutians during 1994–1996 (Estes et al. 1998, 2004).

This study was designed around a more-than-60-year natural experiment associated with the increase and subsequent decline in sea otter populations in the central Aleutian Archipelago. Our inferences were based on previously established effects of sea otters on kelp-forest ecosystems and patterns of covariation in sea otter density and the diets and demography of Bald Eagles. Our field studies were conducted in the early 1990s, when otters were abundant, and in the early 2000s when they were rare. Additional information was available on diets of Bald Eagles from 1936–1937 (Murie 1940), when sea otters were rare, and from 1969–1973 (Sherrod et al. 1976) when they were abundant. Our study design was similar to that used in earlier studies of sea otter–kelp forest interactions (Estes and Duggins 1995) and in numerous other studies that have inferred the effects of apex carnivores on associated species and ecosystem processes (e.g., McLaren and Peterson 1994, Ripple and Larson 2000, Berger et al. 2001, Terborgh et al. 2001, Ripple and Beschta 2006, Myers et al. 2007).

Bald Eagle surveys

We determined productivity and densities of Bald Eagles annually by surveying ~1050 km of shoreline from inflatable skiffs during the nestling phase of the breeding season (early June–early July) during each of two time periods: 1993–1994 and 2000–2002. The 1993–1994 data were from a time when sea otter populations were relatively high but declining, while the 2000–2002 data were from a time period when sea otter populations were extremely low. The Aleutian Islands are treeless, and Bald Eagles nest primarily on sea stacks, pinnacles, and rocky spires in close association with shorelines. Because their nests are exposed and their white heads contrast with the surrounding tundra, we could easily locate nests, count nesting pairs, and determine productivity by counting the number of adults and young in nests. We surveyed essentially the same stretches of coastline once per year for eagles on each of the four islands during each year and determined nesting success (i.e., presence of fully feathered young in nests) and productivity of breeding pairs. We also recorded the number of breeding pairs (i.e., two adults or near-adults within 500 m of a nest site), successful and unsuccessful nests, and single adults. We recorded the number of occupied breeding sites per kilometer of shoreline surveyed to estimate densities. We also recorded clutch size and collected fresh eggs during the egg-laying and incubation stage of the breeding season to describe levels of environmental contaminants (Anthony et al. 1999, 2007).

Eagle diets

We thoroughly searched for prey remains in all of the eagle nests we entered on all four islands during each

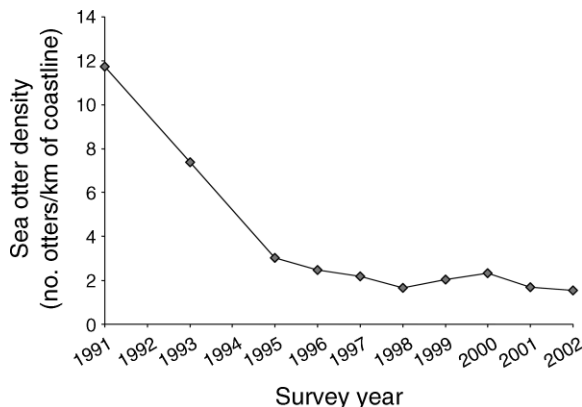


FIG. 1. Density (number of otters per kilometer of coastline) of sea otters near Adak Island, Aleutian Islands, Alaska, USA, 1991–2002.

year of the study (see Plate 1) with the exception of Tanaga, which was not visited in 2001. We searched for prey in >20 nests per island per year and collected a total of 1372 prey remains. We recorded the minimum number of individual prey items determined by the greatest number of identical bones or feathers per prey taxon (Mollhagen et al. 1972, Anthony et al. 1999). We only counted prey remains from active nests that appeared to be from the current-year's nesting attempt, which excluded remains that appeared obviously weathered or deeply soiled. Most avian prey remains were identified by comparison with museum specimens housed at the Alaska Maritime National Wildlife Refuge, Adak, Alaska, USA. We relied on characteristics of fur for mammalian prey because only sea otters and Norway rats (*Rattus norvegicus*) occurred regularly in the diet; caribou (*Rangifer arcticus*) and arctic fox (*Alopex lagopus*) remains occurred infrequently. Fish were identified with Kessler's (1985) guide. Prey remains in nests are known to be somewhat biased toward birds and mammals, but this was the only practical method available for describing diets of Bald Eagles in such a remote area. Furthermore, since the same sampling procedures were used throughout our study and those of Murie (1940) and Sherrod et al. (1976), differences in the data should be indicative of changes in prey availability and eagle diets.

DATA ANALYSIS

Breeding success was calculated as the number of successful nests divided by the total number of occupied territories (i.e., breeding pairs); productivity as the number of feathered young divided by the number of occupied sites; and fledging success as the number of feathered young per successful nest (Postupalsky 1974). Clutch size was recorded as the number of fully feathered young (8–12 weeks old) plus the number of un-hatched or broken eggs in the nest. Some studies have demonstrated that Bald Eagles may abandon nests if disturbed during the incubation phase (Anthony et al.

1994), so we adjusted our estimates of breeding success by excluding a failed nest from calculations of nest success and total number of occupied sites if we had collected a fresh egg from that nest during the incubation phase of that year's breeding season. Similarly, we adjusted productivity, fledging success, and clutch size calculations by adding one young to a successful nest if we collected an egg and the nest was successful during the same breeding season.

We used analysis of variance (ANOVA) with a two-way factorial design to test for differences in clutch size, breeding success, and productivity among islands and study periods. We calculated standardized estimates of nest density (number of occupied breeding territories per kilometer of shoreline surveyed) by including only segments of shoreline surveyed during all years. Unlike our analyses of productivity measures, we used standardized density estimates to account for variable nesting-habitat quality that could influence the number of occupied territories detected during a particular year. Density was calculated only for islands and years where spatially explicit data for the entire standardized survey routes were available. Inclement weather and extremely rough seas resulted in incomplete surveys for Adak, Amchitka, and Tanaga in 1993 and Adak and Amchitka in 2000. Tanaga was not surveyed in 2001 for the same reason. Because we lacked standardized density estimates for all islands each year, we used a repeated-measures ANOVA where island was treated as a random effect to determine if density changed between 1994 and 2002. We used NCSS 2000 (Hintze 2006) for all ANOVA tests.

We summarized and compared proportions of prey remains found in eagle nests by species for each study period. We also compared our results to those of Murie (1940) for 1937 and Sherrod et al. (1976) for 1969–1972 for the same islands and time periods when otters were nearly absent from the Aleutians or very abundant, respectively. We used nonmetric multidimensional scaling (NMS) ordination (Kruskal 1964), a multivariate statistical analysis, to illustrate differences in prey composition between study periods. NMS is well suited for community data because it does not assume linearity among variables and relieves any “zero truncation problems” common to other ordination techniques by using ranked distances (McCune and Grace 2002). Sample units were eagle diets for each island and year combination ($n = 19$ combinations). To minimize the effects of rare and unknown species, species composition was relativized to the major species in the diet, so species occurring in <15% of all samples were excluded from the analysis. Smooth lumpsuckers (*Aptocyclus ventriosus*), a strong outlier ($SD = 2.8$), were also removed from the diet data. Goodness-of-fit of the final NMS model was achieved when stress criterion fell below 15%. We used the multiple-response permutation procedure (MRPP), a nonparametric method, to test whether differences in the proportional makeup of prey

in the diet differed between study periods. We used the Sorensen proportional coefficient (Faith et al. 1987) as the distance measure and reported the A test statistic as a measure of effect size along with the corresponding P values. An $A > 0.0$ indicates less variation within groups than expected by chance. This multivariate analysis avoided all the problems of conducting numerous univariate tests (i.e., inflation of the level of significance, increasing the probability of type I statistical errors). We used PC-ORD (McCune and Mefford 2006) to perform the NMS ordinations and MRPP analysis. We calculated Simpson's index (Krebs 1989) and used bootstrapped confidence intervals to compute prey species diversity in the eagle diet and then tested for differences between study periods using the randomization test described by Solow (1993). We pooled fish and mammalian prey for comparisons of species diversity because only two species of mammals occurred regularly in the eagle diet.

RESULTS

Density and productivity

Density of occupied territories by breeding pairs of Bald Eagles did not change significantly between 1994 and 2002 ($F_{1,3} = 0.27$, $P = 0.64$) but differed among islands ($F_{3,3} = 26.9$, $P = 0.01$). Among all estimates of density, the maximum percentage change of occupied territories between study periods ranged from a 17% decrease at Tanaga to a 16% increase at Amchitka, and these changes counteracted each other in the overall analysis (Fig. 2). Density of occupied territories by breeding pairs was consistently higher throughout the study on Adak (0.41 ± 0.02 pairs/km [mean \pm SE]) and Amchitka (0.42 ± 0.02 pairs/km) compared to Kiska (0.24 ± 0.01 pairs/km) and Tanaga (0.21 ± 0.02 pairs/km).

Clutch size averaged 2.0 eggs/nest and ranged from 1.7 to 2.3 eggs/nest among islands and years (Table 1). Clutch size for this study was high compared to other parts of their range (Buehler 2000). Clutch size did not differ significantly among islands ($F_{3,11} = 1.6$, $P = 0.25$) or study periods ($F_{1,11} = 0.5$, $P = 0.50$). Conversely, average productivity increased significantly from 1993–1994 to 2000–2002 ($F_{1,11} = 29.3$, $P = 0.0002$) and was highest at Amchitka (1.36 young/occupied site) and lowest at Kiska Island (0.98 young/occupied site) ($F_{3,11} = 4.5$, $P = 0.028$). The increase in productivity between study periods was consistent among islands (study period \times island interaction: $F_{3,11} = 1.0$, $P = 0.45$). Breeding success ($F_{1,11} = 3.61$, $P = 0.084$) and fledging success ($F_{1,11} = 4.47$, $P = 0.058$) were marginally higher during 2000–2002 than during 1993–1994, but these estimates were not significantly different among islands ($F_{3,11} < 1.8$, $P > 0.20$). The increase in breeding success (from 65% to 76%) for all islands together and productivity (from 0.98 to 1.36 young/occupied site) between study periods was consistent among islands

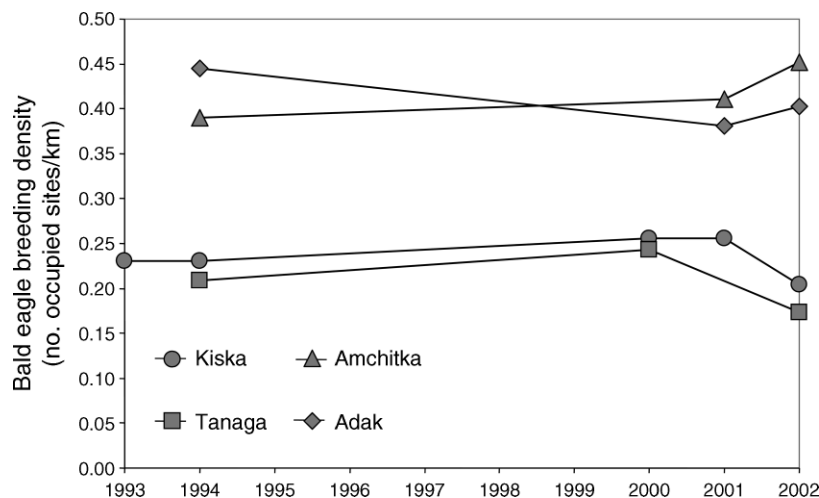


FIG. 2. Density (number of occupied breeding territories per kilometer of coastline) of breeding Bald Eagles on four Aleutian islands, during 1993–1994 and 2000–2002.

(study period \times island interaction: $F_{3,11} < 1.0$, $P > 0.41$).

Diets

We collected and identified a total of 1372 prey remains from Bald Eagle nests during 1993–1994 ($n = 590$ individuals) and 2000–2002 ($n = 782$ individuals). A wide array of mammal, bird, and fish species were present among the remains (Table 2). Norway rats, sea otter pups, Northern Fulmars (*Fulmarus glacialis*), Glaucous-winged Gulls, Pacific cod (*Gadus macrocephalus*), rock greenling, and smooth lumpsuckers collectively comprised 71% of the diet in 1993–1994 (Table 2). Norway rats, Northern Fulmars, Rock Ptarmigan (*Lagopus mutus*), Glaucous-winged Gulls, Pacific cod, rock greenling, and Atka mackerel (*Pleurogrammus monopterygius*) comprised 54% of the diet in 2000–2002. Proportions of fish and mammalian prey decreased by 15% and 11%, respectively, while avian prey increased 26% from 1993–1994 to 2000–2002 (Table 2).

The percentage occurrence of sea otter pups (–13%), rock greenling (–7%), and smooth lumpsucker (–8%) decreased, while Atka mackerel (+5%), Glaucous-winged Gulls (+7%), Rock Ptarmigan (+5%), and unknown birds (+7%) increased in the diet between study periods. The overall composition of the diet in 1993–1994 was similar to that reported for Amchitka Island during 1969–1973 (Sherrod et al. 1976) during which times otters were abundant (Table 2). In addition, our data for 2000–2002 were similar to those reported for the western Aleutian Islands during 1937 (Murie 1940) when only remnant populations of otters existed throughout the Aleutians (Table 2).

The differences in prey species composition between the two sampling periods of our study were exemplified by a three-dimensional nonmetric multidimensional scaling (NMS) that explained 86% of the variation in eagle diets. In addition, the Multiple Response Permutation Procedure (MRPP) provided strong evidence that the proportional makeup of prey in eagle diets shifted

TABLE 1. Comparison of clutch size, nest success, and productivity of Bald Eagles during 1993–1994 and 2000–2002 in the central and western Aleutian Archipelago, Alaska, USA.

Site	Total no. occupied sites surveyed (all fates)		Adjusted clutch size†		Nest success (%)‡		No. young per occupied site†‡		No. young per successful occupied site (fledge success)†‡	
	1993–1994	2000–2002	1993–1994	2000–2002	1993–1994	2000–2002	1993–1994	2000–2002	1993–1994	2000–2002
Western Andreanof Islands										
Adak	69	131	2.1	1.8	72	76	1.09	1.28	1.53	1.68
Tanaga	30	33	2.3	1.9	61	70	0.95	1.34	1.60	1.89
Rat Islands										
Amchitka	37	84	2.0	2.1	72	79	1.22	1.52	1.70	1.91
Kiska	43	86	1.7	1.8	54	77	0.67	1.28	1.30	1.68
All islands	179	334	2.0	1.9	65	76	0.98	1.36	1.53	1.79

† Number of nestlings plus number of eggs present; one young added to nests that were successful subsequent to egg collection.

‡ Excludes nests that failed subsequent to egg collection and unknown fates; weighted mean.

TABLE 2. Diets of Bald Eagles in the Aleutian Islands, from three different studies.

Prey species	Murie (1940)		Sherrod (1976)		This study (1993–1994)		This study (2000–2002)	
	No. prey individuals	% of total	No. prey individuals	% of total	No. prey individuals	% of total	No. prey individuals	% of total
Mammals								
Norway rat (<i>Rattus norvegicus</i>)	1	0.3	43	6.8	48	8.2	41	5.3
Sea otter pup (<i>Enhydra lutris</i>)	0	0.0	100	15.8	90	15.3	18	2.3
Arctic fox (<i>Alopex lagopus</i>)	1	0.3	0	0.0	1	0.2	4	0.5
Aleutian ground squirrel (<i>Spermophilus parryi</i>)	22	6.7	0	0.0	0	0.0	0	0.0
Subtotal	24	7.3	143	22.6	139	23.7	63	8.1
Birds								
Northern Fulmar (<i>Fulmarus glacialis</i>)	74	22.6	42	9.8	49	8.3	55	7.1
Short-tail Shearwater (<i>Puffinus tenuirostris</i>)	13	3.9	10	1.6	19	3.2	22	2.8
Cormorants (<i>Phalacrocorax</i> spp.)	20	6.1	9	1.4	13	2.2	14	1.8
Mallard (<i>Anas platyrhynchos</i>)	0	0.0	6	1.0	7	1.2	10	1.3
Common Teal (<i>Anas crecca</i>)	1	0.3	5	0.8	4	0.7	9	1.2
Long-tailed duck (<i>Clangula hyemalis</i>)	10	3.1	0	0.0	0	0.0	0	0.0
Canada Goose (<i>Branta canadensis</i>)	0	0.0	4	0.6	1	0.2	18	2.3
Common Eider (<i>Somateria mollissima</i>)	4	1.2	13	2.1	5	0.9	13	1.7
Rock Ptarmigan (<i>Lagopus mutus</i>)	1	0.3	26	4.1	16	2.7	59	7.6
Glaucous-winged Gull (<i>Larus glaucescens</i>)	27	8.3	34	5.4	42	7.1	109	14.0
Common Murre (<i>Uria aalge</i>)	22	6.7	16	2.5	8	1.4	13	1.7
Pigeon Guillemot (<i>Cephus columba</i>)	4	1.2	1	0.2	5	0.8	8	1.0
Ancient Murrelet (<i>Synthliboramphus antiquus</i>)	9	2.8	36	5.7	5	0.8	29	3.7
Auklet spp. (<i>Aethia</i>)	48	14.8	57	9.0	18	3.1	24	3.1
Tufted Puffin (<i>Fratercula cirrhata</i>)	21	6.4	25	4.0	13	2.2	24	3.1
Horned Puffin (<i>Fratercula corniculata</i>)	13	4.6	11	1.7	0	0.0	0	0.0
Other species†	12	3.7	25	4.0	21	3.6	41	5.3
Unknown birds	1	0.3	17	2.7	7	1.2	70	9.0
Subtotal	280	86.3	361	57.1	233	39.6	518	66.2
Fish								
Pacific cod (<i>Gadus macrocephalus</i>)	1	0.3	3	0.5	65	11.0	67	8.6
Rock greenling (<i>Hexagrammus lagocephalus</i>)	4	1.2	68	10.7	79	13.4	51	6.7
Atka mackerel (<i>Pleuragrammus monopterygius</i>)	9	2.8	0	0.0	2	0.3	40	5.1
Smooth lump sucker (<i>Aptocyclus ventricosus</i>)	0	0.0	19	3.1	45	7.6	1	0.2
Dolly varden (<i>Salvelinus malma</i>)	1	0.3	6	1.0	10	1.7	3	0.4
Other species‡	4	1.2	13	2.1	12	2.0	17	2.2
Unknown fish	2	0.6	17	2.7	4	0.7	22	2.8
Subtotal	21	6.4	126	20.3	217	36.7	201	25.7
Total	325	100	630	100	589	100	782	100

† Other birds: Fork-tailed Petrel (*Oceanodroma furcata*), Emperor Goose (*Chen canagica*), Pintail (*Anas acuta*), Harlequin Duck (*Histrionicus histrionicus*), Red-breasted Merganser (*Mergus serrator*), Bald Eagle nestling (*Haliaeetus leucocephalus*), Peregrine Falcon (*Falco peregrinus*), Glaucous Gull (*Larus hyperboreus*), Black-legged Kittiwake (*Rissa tridactyla*), Rock Sandpiper (*Calidris pilocnemis*), Parasitic Jaeger (*Stercorarius parasiticus*), Black Oystercatcher (*Haematopus bachmani*), Laysan Albatross (*Diomedea immutabilis*), Short-eared Owl (*Asio flammeus*), Snow Bunting (*Plectrophenax nivalis*), Common Raven (*Corvus corax*).

‡ Other fish: longnose lancet fish (*Alepisaurus ferox*), filamented grenadier (*Coryphaenoides filifer*), rockfish (*Sebastes* spp.), red Irish lord (*Hemilepidotus hemilepidotus*), armorhead sculpin (*Gymnocanthus galeatus*), lobefin snailfish (*Polypera greeni*), Greenland halibut (*Reinhardtius hippoglossoides*).

significantly between the two sampling periods ($A = 0.04$, $P = 0.0005$). Eagle diets during the two study periods were clearly distinct in three-dimensional ordination space (Fig. 3), and there was more variability in diets between sampling periods than among years within sampling periods (Appendix). Diets during 1993–1994 were associated with sea otter pups, rock greenling, and rockfish (*Sebastes* spp.), whereas diets during 2000–2002 were associated with Glaucous-winged Gulls, Tufted Puffins (*Fratercula cirrhata*), Rock Ptarmigan, Northern Pintails (*Anas acuta*), and Common Eiders (*Somateria mollissima*). The diversity of prey species in the diet increased significantly from 1993–1994 to 2000–2002 at all islands with all taxa combined ($P \leq 0.02$, Fig.

4). This increase was primarily due to the increase in diversity of fish and mammalian prey during 2000–2002.

DISCUSSION

Bald Eagles occur at high population densities westward across the Aleutian Archipelago to Kiska and Buldir Islands, the western extent of their breeding range. Throughout this region they nest on islets, coastal cliffs, or sea stacks and feed mainly on marine organisms (Murie 1940, Sherrod et al. 1976). Most of their prey (>90%) come from the nearshore marine community (Anthony et al. 1999). This strong dependence on the marine environment is not surprising, given the region's highly productive oceans and comparatively unproduc-

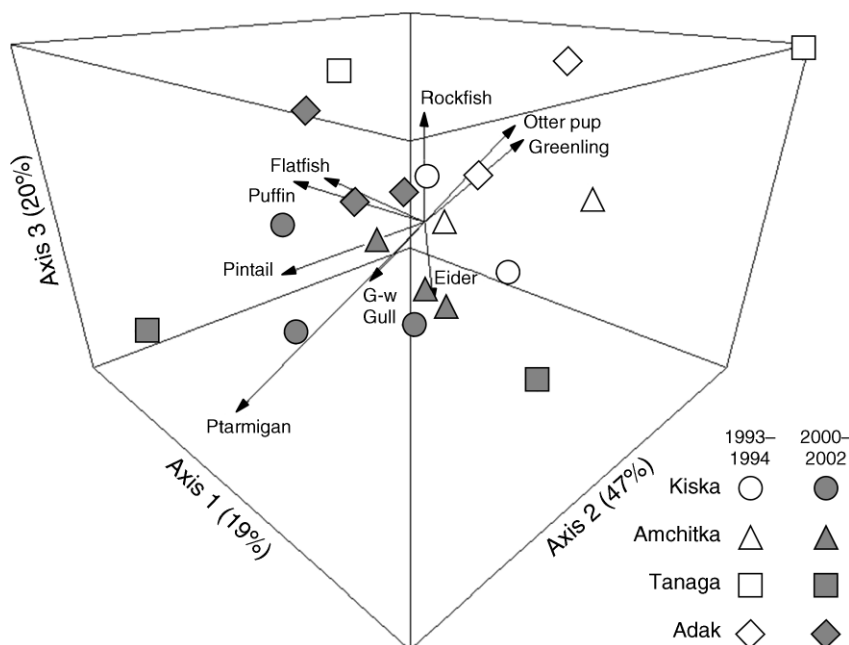


FIG. 3. Ordination of prey items in Bald Eagle nests from the four study islands in the Aleutian Archipelago, Alaska, during 1993–1994 and 2000–2002 with nonmetric multidimensional scaling. Sample units are eagle diets from Rat Islands (Kiska, Amchitka) and Andreanof Islands (Tanaga, Adak) for each sampling period.

tive terrestrial systems (Croll et al. 2005). The Bald Eagle's dependence on food from the coastal marine environment predisposes the species to indirect effects from trophic cascades induced by the presence of sea otters. Any such effects should be evident as temporal changes associated with the recent decline of otter populations and collapse of the kelp-forest ecosystem. Our data on diets and productivity were spatially extensive and spanned the critical time period of sea otter abundance and subsequent decline, thus providing evidence for these indirect effects. In addition, Bald Eagles are opportunistic in their foraging habits (Watson et al. 1991), and their diets reflect the abundance and availability of their prey within the limits of their ability to capture such prey (Buehler 2000). Consequently, we believe that the changes in diets we observed reflected the influence of sea otters on the abundance of the eagle's prey in the nearshore marine ecosystem.

Coastal ecosystems in the west-central Aleutian Archipelago changed markedly between the early 1990s and early 2000s, the two time periods during which we were able to investigate demography and diets of Bald Eagles. Sea otter populations declined during this period (Doroff et al. 2003, Estes et al. 2005), as did the distribution and abundance of kelp (Estes et al. 2004) and kelp-associated species (Reisewitz et al. 2006). Diets of Bald Eagles during 1993–1994 vs. 2000–2002 changed dramatically, supporting our initial prediction. Sea otter pups and rock greenling were both important eagle prey prior to and during the early period of the sea

otter decline. After the decline of otter populations during the late 1990s, the percentage occurrence of rock greenling and sea otter pups in the diet declined by twofold and sevenfold, respectively. In contrast, remains of Rock Ptarmigan, Glaucous-winged Gulls, and other seabirds in eagle nests increased by 25%, and those of Atka mackerel increased by 5%. The dietary composition of Bald Eagles during 1993–1994 was similar to that reported by Sherrod et al. (1976) for Amchitka Island in the early 1970s, a place and time in which sea otters and kelp were also abundant. The diet during 2000–2002 was similar to that in 1937 (Murie 1940) when sea otters

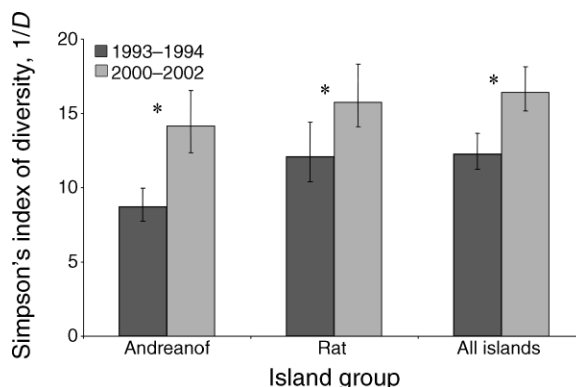


FIG. 4. Diversity (Simpson's index [$1/D$ and 95% CI]) of prey in Bald Eagle nests in the Andreanof and Rat Islands during 1993–1994 and 2000–2002. Asterisks indicate significant differences ($P < 0.05$) in prey diversity between sampling periods.



PLATE 1. The first author (Anthony) finds himself eye-to-eye with an aggressive eaglet as he checks its nest for prey remains, Adak Island, Aleutian Archipelago, Alaska, 2002. Photo credit: Norm Smith.

existed as small, remnant populations in a small portion of the Archipelago. These changes in diets of Bald Eagles appear to have resulted from changes in prey availability that ultimately were caused by the sea otter/kelp forest collapse. Because our sampling efforts and those of Sherrod et al. (1976) were conducted over several years, it does not appear that the differences we observed were a result of annual fluctuations in the diet (see Appendix).

Coastal ecosystems in the Aleutian Archipelago have undergone other significant changes besides those associated with the sea otter decline, and these factors must be considered as alternative explanations to the changes in eagle diets. Climatic and oceanographic changes associated with the Pacific Decadal Oscillation and removal of arctic fox deserve consideration. The Pacific Decadal Oscillation caused an abrupt warming in the late 1970s and more modest cooling in the mid-1990s (Mantua and Hare 2002). Arctic foxes were introduced to most of the Aleutian Islands following the collapse of the maritime fur trade in the early 1900s (Bailey 1993), but were removed from all of the islands during the last several decades to restore the region's avifauna (Bailey 1993, Byrd et al. 1994). Although it is difficult to assess the influences of ocean climate change or the fox removals on Bald Eagle foraging ecology, neither appear to provide a compelling alternative explanation to the sea otter/kelp forest model.

First, the last regime shift in oceanic conditions occurred in the 1970s (Mantua and Hare 2002), well before the recent decline in otter abundance and our two sampling periods. Similarly, the timing of removal of arctic foxes did not correspond with the changes in eagle diets that we observed. The U.S. Fish and Wildlife Service removed foxes from Amchitka Island in 1961 and Kiska Island in the mid-1980s well before our study, and most were removed from Tanaga and Adak in 2001 toward the end of our study (V. Byrd, *personal communication*). Based on the timing of the fox removals from the four islands, it appears that the fox removals would have had little to no effect on our comparison of eagle diets between 1993–1994 and 2000–2002. This argument is supported by the lack of any overall changes in density of breeding seabirds in the Aleutian Islands during the period of our study (Dragoo et al. 2004). In addition, earlier published reports on eagle diets (Murie 1940, Sherrod et al. 1976) from the Aleutian Archipelago are consistent with our explanation.

Although the collective diet data available for Bald Eagles over the 60-year period provides evidence for a food-web linkage between Bald Eagles and sea otters, other dietary changes of eagles occurred that were apparently unrelated to the sea otter–kelp forest collapse. At least two such changes were evident in our dietary data. First, large numbers of smooth lumpsuckers briefly appeared in shallow coastal waters across the

central and western Aleutians during the late winter/early spring of 1991–1992 and 1992–1993 (Watt et al. 2000). A similar phenomenon was reported in the mid-1960s (Kenyon 1969). Apparently, smooth lumpsuckers, which typically occur in oceanic waters (Yoshida and Yamaguchi 1985, Il'inskii and Radchenko 1993), episodically migrate to the coastal zone to spawn (Watt et al. 2000). Lumpsuckers, which were among the more common prey remains in eagle nests during 1993 (22% of the fish, 8% of the total; Appendix), were absent during the early 2000s. Second, in contrast to the rock greenling and smooth lumpsucker declines, Atka mackerel populations apparently increased greatly over this same time period (Lowe et al. 2006). Atka mackerel were never observed in the many hours we spent diving and boating in the Aleutian Islands from 1970 through the mid-1990s (J. A. Estes, *personal observations*), nor were they reported in eagle diets in the early 1970s (Sherrod et al. 1976). By the late 1990s, they had become exceedingly abundant in these same areas, often appearing as vast schools that extended over many hectares, from the ocean's surface to the seafloor (J. A. Estes, *personal observations*; K. Bell, *R/V Tiglax*, *personal communication*). As was true for the lumpsuckers, reasons for the Atka mackerel increases do not appear to be directly associated with the sea otter–kelp forest collapse. Potential explanations include changing oceanographic conditions or the release from predation by Steller sea lions (*Eumetopias jubata*) and harbor seals (*Phoca vitulina*), which declined markedly throughout this region in the decade preceding the sea otter decline (National Research Council 2003, Springer et al. 2003). Regardless of the cause, the large population increase in Atka mackerel was observed in the eagle's diet. Atka mackerel were nearly absent from eagle-nest remains in the mid-1990s, but by the early 2000s they comprised 19% of the fish and 5% of the total prey remains. The precipitous decline in smooth lumpsuckers and increase in Atka mackerel during our study basically counteracted each other in the overall analysis of eagle diets (i.e., a net decrease in fish remains of 3%).

Because of the kelp-forest decline and related changes in prey availability that occurred over the time period of our study, we predicted declines in density and productivity of Bald Eagles. We expected these declines because the kelp-forest collapse would have resulted in a 2–3 fold reduction in total productivity within the kelp forest community (Duggins et al. 1989). However, our data provided no indication that densities changed between the two time periods, although nesting densities varied two-fold among islands groups. Clutch size also was similar between these two time periods. In contrast to our initial predictions, nesting success and productivity increased from 1993–1994 to 2000–2002 at all of the islands. The reason for the increase in productivity is not clear but may be a result of increased nutrition resulting from more seabirds in the eagle's diet. Birds such as waterfowl are rich in lipids and therefore have a

higher nutritional value per unit mass than do fish (Stalmaster and Gessaman 1984), so the increase of birds in the eagle's diet from 1993–1994 to 2000–2002 may have resulted in better nutritional condition and higher reproductive success following the otter decline. Another possible explanation for the increase in productivity may be a reduction in environmental contaminants, which was observed at Kiska Island in the early 1990s (Anthony et al. 1999). However, the increase in productivity occurred at all four islands, and concentrations of contaminants in Bald Eagle eggs were below threshold levels for effects on productivity (Elliott and Harris 2001) at all islands and during all years except for Kiska in 1993–1994 (Anthony et al. 2007). Consequently, it does not appear that reduced levels of contaminants were responsible for the increase in productivity between our two sampling periods.

In contrast with the declining mammals and kelp-forest fishes, seabird numbers were apparently unaffected by the kelp-forest collapse. While Glaucous-winged Gulls feed extensively in the intertidal zone and adjacent nearshore waters, they also are capable of responding to the sea otter-induced trophic cascade through dietary shifts (Irons et al. 1986), so they have remained abundant in the Aleutian Islands throughout the period of the sea otter decline. The proportion of Glaucous-winged Gulls in the eagle's diet increased twofold between our two study periods. In general, seabirds by virtue of their extreme mobility are capable of obtaining nutritional resources over areas that extend well beyond the coastal kelp-forest ecosystem. Consequently, Bald Eagles appear to have responded to the reduced production and prey availability in coastal waters that resulted from the kelp-forest collapse by acquiring a greater proportion of their prey from offshore production. This exemplifies further the opportunistic nature of their foraging behavior.

Our findings provide further evidence for wide-ranging indirect effects of sea otters on nearshore marine communities. This top-down effect of sea otters traversed several species and trophic levels to another apex predator, the Bald Eagle. Similarly, a top-down effect of cougars on riparian systems in Zion National Park, USA, traversed five species and four trophic levels to butterflies and fish (Ripple and Beschta 2006). A top-down effect of wolves in Banff National Park, Canada, traversed four species and three trophic levels to beaver and songbird populations (Hebblewhite et al. 2005). Berger et al. (2001) provided empirical support for a top-down effect of wolves and grizzly bears in the Greater Yellowstone ecosystem of the western United States that traversed four species and three trophic levels to songbird populations. In our study, the interaction chain transcended five species and four interspecies linkages—from sea otters to sea urchins to kelp to fish to Bald Eagles. To our knowledge, such an indirect effect of one apex predator on another through such a complex trophic pathway has not been described

previously. Our findings more broadly imply that interaction strengths from top-down effects can be maintained across relatively long and complex pathways of interspecies linkages.

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APPENDIX

A table summarizing annual diets (number of prey items and percentage of total) of Bald Eagles at Adak, Amchitka, Kiska, and Tanaga islands, Aleutian Archipelago, Alaska, 1993–1994 and 2000–2002 (*Ecological Archives* E089-154-A1).